

The Effects of Intertidal Height and the Parasitic Crustacean *Fabia subquadrata* Dana on the Nutrition and Reproductive Capacity of the California Sea Mussel *Mytilus californianus* Conrad

BY

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(2 Text figures)

INTRODUCTION

Fabia subquadrata Dana, 1851 (Arthropoda : Pinnotheridae) has been observed in many different pelecypod hosts on the Pacific coast, from southern California to Alaska, including *Mya arenaria* Linnaeus, 1758 (RATHBUN, 1918), *Mytilus edulis* Linnaeus, 1758 (WELLS, 1928), *Mytilus californianus* Conrad, 1837 (RICKETTS & CALVIN, 1968), and *Modiolus modiolus* (Linnaeus, 1758) (PEARCE, 1966). Immature stages have been observed (PEARCE, 1966) in other lamellibranch genera, including *Astarte*, *Cardita*, *Crenella*, and *Kellia*. While the infestation rate of *M. californianus* beds varies somewhat, it is usually found to be approximately 3% (RICKETTS & CALVIN, *op. cit.*). This may actually be an underestimation owing to the small size of the male "pea crab" and the consequent ease with which it may be overlooked in the mussel. Additionally, the male (according to RATHBUN, 1918 [see description of *Pinnotheres concharum*] and LIGHT *et al.* 1970) may occasionally be found outside the host (though this is disputed by PEARCE, 1966) and therefore missed in many collections. The mature, yet soft-bodied female of the species seems to live by orienting herself on either the right or left gill, clasping several gill filaments, and feeding by drawing the mucous food strings produced by the host into its mouth.

Many known hosts of the Pinnotheridae have been listed by RATHBUN (1918), and CHENG (1967) has

recently amended the list. WELLS (1940) summarized early discussions of the nature of symbiotic relationships among the pinnotherids. PEARCE (1966) presented the first detailed account of the biology of *Fabia subquadrata* with emphasis on its highly modified reproductive pattern; he concluded that except during reproductive swarming, the crab must be associated with a host, and that adaptations to the symbiotic mode of life are many and extensive. CHRISTENSEN & McDERMOTT (1958) noted many similar modifications present in another symbiotic pinnotherid, *Pinnotheres ostreum* Say, 1817. RATHBUN (*op. cit.*) characterized several pinnotherids as "commensals" in "bivalve mollusks"; MACGINITIE & MACGINITIE (1949) concur, noting the family is characteristically commensal. LIGHT *et al.* (1954) note that *F. subquadrata* is "commensal in *Mytilus*" and yet PEARCE (*op. cit.*) believes, on the basis of tissue damage, that in *Modiolus modiolus* *F. subquadrata* is parasitic. Tissue erosion has also been observed in two pelecypod hosts of *Pinnotheres ostreum*, *Crassostrea virginica* (Gmelin, 1791) (STAUBER, 1945; SANDOZ & HOPKINS, 1947) and *Mytilus edulis* (McDERMOTT, 1962). To be resolved are the questions of what biological consequences of this tissue damage to the bivalves may be and what the specific nature of the *Mytilus* - *Fabia* relationship is.

It is generally agreed (for example, GIESE & ARAKI, 1969; GALTISOFF, 1964; LAWRENCE *et al.*, 1965; WILBER & GILCHRIST, 1965) that body component indices

$$\frac{(\text{wet weight of component} \times 100)}{\text{total body weight}}$$

are fairly reliable indicators of both the general health

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of many invertebrates and of their immediate biological priorities. Thus GIESE & ARAKI (1962) have determined the reproductive cycles of 2 intertidal chitons by following their respective body component indices and SCHEER (1940) has evaluated the nutritional value of various diets for *Mytilus californianus* by observing changes in relative body component weights through prolonged feeding experiments. This method was also applied to Oregon intertidal populations of the purple sea urchins *Strongylocentrotus purpuratus* (Stimpson, 1857) by GONOR (1972), who observed asynchronous reproductive activity in populations of different habitats and age structures.

In conjunction with glycogen determinations and estimations of gamete numbers, body component indices were used to study the *Mytilus californianus* - *Fabia subquadrata* relationship. The apparent competition between the host mussel and the symbiotic pinnotherid for nutrients and the damage inadvertently done the mussel suggest that *F. subquadrata* is not merely a commensal pea crab sharing filtered food with its host, but rather a true parasite which causes damage considerably more extensive than that previously reported. The present study examines this hypothesis.

MATERIALS AND METHODS

Four widely separated *Mytilus californianus* populations along the exposed rocky intertidal zone of the Sonoma County, California coastline were each sampled twice, two samples taken 29 April, 1972, and the others in succeeding one-week intervals throughout May, 1972, a period of intense reproductive activity (BARTLETT, 1972). Each sample consisted of several hundred mussels taken between approximately - 0.3m and + 0.3m (referred to as "lower zone") and another group taken between approximately + 0.9m and + 1.5m ("upper zone"). Tidal data are given in reference to mean lower low water. Collection stations were Ocean Cove (38°33'40"N), MiWok State Beach (38°23'20"N), Portuguese State Beach (38°23'N), and Windmill Beach (38°18'15"N).

Specimens were either opened immediately or removed to the laboratory and held in running seawater until examined. Of those maintained in the laboratory, most were examined within 2 or 3 days of collection; none was examined after more than 5 days holding. Individual mussels were scraped to remove all material from the exterior of the valves. The posterior adductor muscle was bisected and the fluid of the mantle chamber allowed to drain. In turn the gills, gonads, and remaining viscera

were dissected out, daubed on absorbent paper to remove most of the adsorbed fluid, and weighed to the nearest hundredth gram. The valves were weighed and their volume determined by filling them to capacity with a known volume of water. The various organs were dried to constant weight at 85° C, weighed, and their original water levels determined by difference. Body component indices were determined by dividing the wet weight of the component in question by the wet weight of the entire soft body and multiplying by 100. The soft body index is that percentage of the intact mussel's weight attributable to all parts excepting the shell; correspondingly, the shell index is that portion of the intact mussel's weight attributable to valves and ligament. When an infested mussel was dissected, several others of similar length and width were chosen for comparison in order that differences due to size alone might be minimized.

Glycogens (STETTEN & STETTEN, 1960) were extracted from entire soft-bodies (dried, macerated, and digested with 30% w/v KOH) and determined as glucose after treatment with 0.2% anthrone reagent by measuring absorbance at 620nm with a Beckman spectrophotometer (see SEIFTER *et al.*, 1950).

Early in the investigation, it was noted that obvious differences existed between mussels with respect to their reproductive conditions. BARTLETT (1972) conducted his study during a period of very active spawning in *Mytilus californianus* and showed that it is likely that most individuals whose gonads appeared flaccid had recently discharged gametes. While some appeared "spawned out" and showed relatively little gonadal tissue in the mantle, others were obviously ripe with gametes. While a highly accurate determination of seasonal gonadal development might have been obtained by the method of CHIPPERFIELD (1953), lack of time dictated a more rapid assessment. Those individuals whose gonads appeared thick and displayed motile sperm or ripe ova were selected for dissection, while those that appeared flaccid or spawned out, whether infested or not, were discarded.

To relate the gonad indices obtained as described above more closely to potential for reproduction, periodic sperm counts were made. These were accomplished by removing as much adsorbed water as possible from gonadal tissue, weighing and then macerating the tissue in a Waring blender with a known volume of seawater. Sperm were counted on a haemocytometer and counts multiplied by the dilution factor. No attempt was made to differentiate between the various developmental stages of the sperm. This method is not suitable for counting ova as they do not remain intact in a blender.

Data are based only on mussels from 70mm to 99mm in length; variance due to difference in age is thereby minimized (GONOR, 1972), as very nearly all mussels of this size are sexually mature (COE & FOX, 1942), individuals of this size are distributed over nearly the entire intertidal range, and a high rate of infestation occurs among them, allowing obtainment of a sufficiently large sample. Of 111 mussels (of appropriate size and reproductive condition) indexed, as described above, 41 contained *Fabia subquadrata*. Significance, as used below, was determined by Student's "t-test" and indicates $p \leq 0.05$.

RESULTS

Differences Between Mussels of Upper and Lower Sampling Zones

As indicated in Figure 1, unfested mussels of the upper zone display a significantly lower shell index than do lower zone unfested mussels. This relationship was ob-

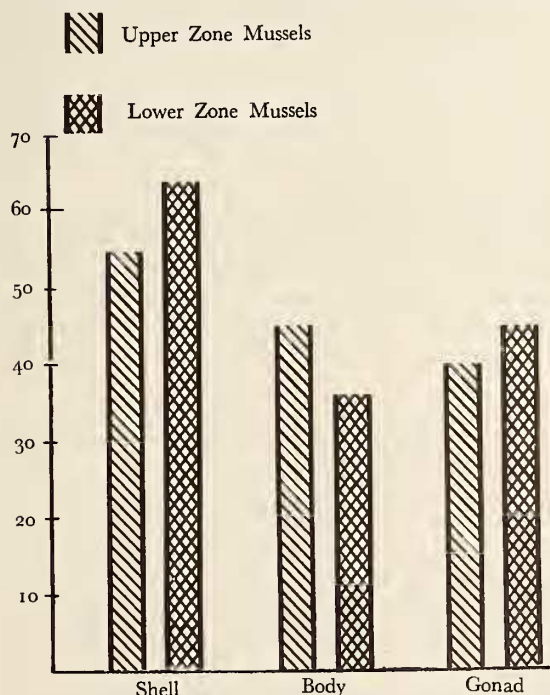


Figure 1

The bar diagram depicts differences observed in shell, body, and gonad indices (see text) in unfested mussels sampled from high and low intertidal sites. The index of each component is read from the vertical axis

served at 3 of the 4 sampling sites. At the remaining site, a large, nearly vertical rock face at Portuguese State Beach, there was no significant difference observed between mussels distributed over a vertical elevation of approximately 1.7m. At all sites, excepting Portuguese State Beach, the mean lower zone shell index was 64, while the upper zone mean index was 55. The corresponding soft body indices were therefore 36 and 45, respectively. The ratio of grams of soft body to milliliters of shell volume was constant throughout the intertidal zones assayed, and of mean $0.054 \text{ dry gm ml}^{-1}$ or $0.39 \text{ wet gm ml}^{-1}$ (Table 1).

Table 1

Mean Weight-to-Volume Ratios

Length (mm)	Volume (ml)	Wet Ratio	Dry Ratio
70-79	25	0.39	0.054 ± 0.02
80-89	37	0.39	0.045 ± 0.03
90-99	50	0.36	0.053 ± 0.03

N = 70

At Portuguese Beach the mean shell index was 66. The peculiarities of this sampling site will be discussed in the following section. Suffice it to say here that vertical height seems not always to be a valid index of tidal exposure. Portuguese Beach data were not pooled with data from the other sampling sites for statistical computations.

One other consistent difference was found between mussels of the upper and lower zones. Those of the higher intertidal levels had a mean gonad index of 40, while those of the lower zone had a significantly higher index of 45.

Effects of Infestation

At none of the lower zone sites was there any significant difference of body component indices between infested and non-infested mussels. However, the mussels from the higher zones were consistently found to have indices which differed significantly in several important ways (Figure 2 and Table 2) from their unfested neighbors.

1) **Ripe Gonad Index:** As mentioned above, only individuals with gonads which were judged to be "ripe" have been included in the present data and therefore the term "ripe gonad index" is used to prevent confusion with other published data. It was observed that while the

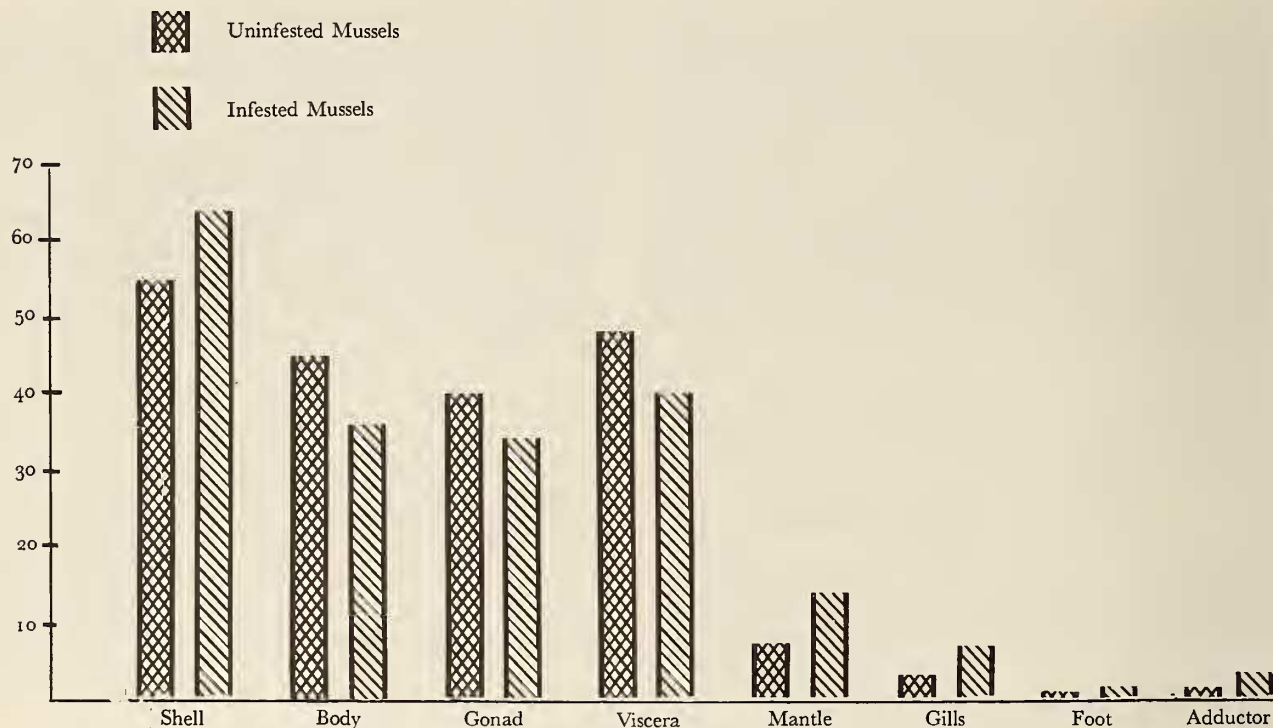


Figure 2

The diagram illustrates differences observed in shell, body, and body component indices of infested and uninfested mussels collected at upper intertidal zone sites. Indices (see text and Table 2) are read from the vertical axis

Table 2

The Effects of Infestation on Body Component Indices of Upper Zone *Mytilus californianus*

Means and Variances of Component Indices						
	Water Level	Uninfested Mussels n = 38		Infested Mussels n = 23		t _s ¹
Shell	—	55	221.70	64	251.48	2.233 ²
Body	81.5%/79.9%	45	214.96	36	243.68	2.268 ²
Gonads	83%	40	78.26	34	85.35	2.525 ²
Viscera	82.5%	48	92.77	40	80.68	3.223 ³
Mantle	73%	07	60.10	14	54.69	3.467 ³
Gills	72%	03	31.82	07	32.70	2.670 ²
Foot	75%	0.5	29.66	1.7	34.78	0.808 ⁴
Adductor	70%	1.5	12.63	3.3	8.88	2.033 ²

¹ t_s values calculated using Student's test for comparison of means

² $P \leq 0.05$; ³ $P \leq 0.01$; ⁴not significant

mean ripe gonad index of uninfested mussels was 40, the mean index of their infested neighbors was significantly less at 34.

2) **Viscera Index:** Viscera indices (by weight, the viscera consist chiefly of digestive gland, pedal retractor muscle, and gut) among infested and uninfested upper zone mussels differed similarly; the mean index of infested individuals was found to be 40 and that of uninfested specimen to be 48.

3) **Soft Body Index:** The increase in body index with increasing intertidal height was noted above. The mean body index of upper zone uninfested mussels is significantly greater than the mean of infested upper zone mussels; the former was found to be 45 and the latter 36.

4) **Spermatogenesis:** While there was much variation between different mussels, and even between different samples from the same mussel, a mean of 2.1×10^8 sperm gm^{-1} was calculated. No significant differences could be detected between the different tidal zones or between infested and uninfested individuals.

5) **Glycogen Levels:** Perhaps one of the most conspicuous differences between infested and uninfested individuals was seen in their respective glycogen levels, 5% dry weight and 17% dry weight. This represents a decrease in whole-body carbohydrate reserve material of 76%.

6) **Water Levels:** Total body water levels were 81.5% and 79.9% for uninfested and infested mussels, respectively. However, the disparity of 1.6% apparently results not from differences in the water content of the several organs but rather from differences in the relative weight contributions of the organs of the body as a whole.

DISCUSSION

Data from Portuguese State Beach

As has been noted above, the mussels collected at Portuguese State Beach do not show any of the variation between tidal levels typical of those at the other 3 sites. The actual collection site was a large rock, the nearly vertical face of which provided an attachment site for thousands of mussels. It has been noted during collection at a low tide (-0.15m) that even relatively small waves washed very high up onto the rock and occasionally reached the top. It has been surmised that because of its particular orientation relative to predominant wave and wind directions, and its consequently more frequent wet-

tings, it is less affected by changes in tide than are others. It therefore does not yield data consistent with those from areas greatly affected by periodic tidal fluctuations.

Shell Indices: A difference was noted among the shell indices of upper and lower zone mussels. Data presented for lower zone shell indices conform fairly well with those given for northern California mussels ($38^{\circ}31'N$) by RAO (1953a). Differences observed between upper and lower zone mussels are of a magnitude comparable with that reported by RAO (1953b) for southern California intertidal populations. Because the shell index and soft body index are mutually dependent, data presented here showing higher shell indices in lower zone mussels might be interpreted as indicating there is less tissue weight rather than more shell weight in lower zone mussels. The contention is vitiated, however, by the observation made above that the ratio of tissue weight to shell volume is independent of tested tidal heights (Table 2). Therefore, assuming comparable densities, the shells of lower zone mussels must be thicker than those of upper zone mussels. RAO (1953b) suggests that the observed increase in relative shell weight is due to increased exposure to calcium ion in seawater solution as a consequence of lower intertidal height. FOX & COE (1943) noted differences in thickness and relative dimensions of the shells of mussels grown on rocks and piers. While intertidal height was not specified, their observations seem to indicate that there are environmental factors other than calcium availability which significantly affect shell growth. It may also be that energetic limitations with which high-intertidal mussels must cope make extensive shell growth bioenergetically uneconomical.

Differences in Body Component Proportions: It is apparent that an important stress on *Mytilus californianus*, and on any other filter feeding organism inhabiting the upper intertidal zone, is the markedly reduced time available for food gathering. Also, the upper zone animal must retain, during low tide, what water it can until the supply can be renewed with the next high tide. In the Bivalvia, water is often stored simply by tightly sealing the valves and mantle. This behavior is characteristic of *M. californianus*. Effectively isolated from its environment by its clamped valves, the mussel rapidly decreases the oxygen tension of the enclosed fluid (MOON & PRITCHARD, 1970) and must concomitantly reduce its oxygen consumption. Maintenance of any particular level of metabolism, therefore, would require increased reliance on anaerobic respiration. As GODDARD & MARTIN (1966) point out, while anaerobic respiration may be efficient in terms of the ratio "energy extracted : energy consumed in extraction" it may be wasteful in that much of the energy

and many of the nutrients at hand cannot be extracted and utilized; it would seem that an organism upon whose food availability strict limits have been placed would suffer more from this wastage than one to which sufficient food stuffs were available. Many mollusks undergoing hypoxic stress therefore retain glycolytic metabolites and utilize them aerobically when oxygen again becomes available. Investigations by various authors have demonstrated, either directly through detection of accumulated lactate or inferentially by observation of repayment of an "oxygen debt" that at least some marine lamellibranchs make this chemical economy. *Mya arenaria* Linnaeus, 1758 has been found by VAN DAM (1935) to build up an oxygen deficit during exposure for which it compensates upon reimmersion both by increasing the rate at which water is pumped through the mantle cavity and the efficiency with which oxygen is assimilated. Using *Mytilus edulis* Linnaeus, 1758, SCHLEIPER (1959) has shown that oxygen debts are repaid both by individuals and individual tissues, and that the process is very slow. MOON & PRITCHARD (1970) detected lactate accumulation in exposed *Mytilus californianus* and an exposure-time dependent increase in oxygen consumption upon reimmersion. Accumulation of an oxygen debt, particularly because of the time lag in repayment which may be involved, would seem only to compound the high-intertidal mussel's problems, for maximum metabolic efficiency must be important when many metabolic obligations are to be dispatched in the relatively short duration of a very high tide. Another metabolic problem is incurred by frequent exposure to air in northern California mussels. It is known that while sea water temperatures in this area are fairly low (usually 10° to 16° C) and constant year-around, and therefore keep a submerged mussel at approximately ambient temperature, exposure to air and direct sunlight, particularly of a gray-black shell, must greatly increase the tissue temperature and thereby the respiratory rate. WIDDOWS & BAYNE (1971) have shown that in *M. edulis*, although long-term (ca. 14 days) temperature acclimation may occur, increased temperature causes an initially large rise in metabolic rate ($Q_{10}^{(5^{\circ}-15^{\circ})}$ [winter] = 3.7; $Q_{10}^{(10^{\circ}-20^{\circ})}$ [summer] = 3.3); moreover, they believe that increased temperature is an important, though transient, physiological stress on the mussel and BAYNE (1973) interpreted an observed rise in blood-sugar levels as possibly indicating mobilization of reserve materials to deal with the energy imbalance created by warming.

In many mollusks, as the ratio of anaerobiosis : aerobiosis increases, the amount of carbohydrate metabolized per unit time increases. For example, WERNSTEDT (1944) has shown that in the gill epithelium of the freshwater mussel *Dreissena* sp., glycogen consumption is 3 times

greater under anaerobic than aerobic conditions. This is reasonable in that anaerobically more carbohydrate must be consumed in the liberation of energy at any given rate, and has been termed the "Pasteur effect." While it seems at least plausible that an aestivation-like response might occur in *Mytilus californianus*, the findings of MOON & PRITCHARD (1970: 38) indicate that this is likely not the case.

With these, and possibly other "metabolic disadvantages" to contend with, one might expect to observe some indications of energetic or nutrient stress, or both, in upper tidal zone mussels. It has been shown by several investigators that when bivalves are starved, become diseased, or are stressed seriously in some other way, often one of the first responses is a reduction of energy and nutrients devoted to their reproductive effort (as determined by gonadal weight relative to total weight or volume of organism) (SCHEER, 1940; COE & FOX, 1942; FOX & COE, 1943; GALTISOFF, 1964). From the data above, it seems that in the face of a severely limited nutrient supply and increased metabolic demands, the response of upper zone *Mytilus californianus* is reduced gonadal development. This is indicated by the ripe-gonad index of upper zone mussels which is significantly lower than that of lower zone specimens, mussels which presumably do not suffer such strains. That May, 1972 was, in fact, a favorable time during which to judge reproductive effort by gonadal weights has been shown by BARTLETT (1972) who has investigated reproductive synchrony in local *M. californianus* populations and found intense reproductive activity during April, May, and June of that year.

The Effects of Infestation: The effect of *Fabia subquadrata* infestation on *Mytilus californianus* appears to be an exaggeration of the effects suffered by uninfested upper zone mussels. Firstly, if food is in short supply for the non-infested upper zone mussel, the nutrient strain on an infested mussel must be much greater in that it has been seen that the actively feeding pea crab deprives the host of its mucous string of entrapped food particles. Secondly, oxygen tension, critical to mussels, but especially to those of the upper tidal zones in view of its aforementioned effect on metabolic efficiency, could only be decreased more rapidly by a symbiotic crab respiring within the mantle cavity.

Ctenidial erosion is another consequence of pea crab infestation. Not only must continual tissue repair be supported by a clearly limited intake of energy, but there is likely also some lessening of filtering efficiency due to interference with ciliary currents and, consequently, with the movement of food-laden mucus in the damaged regions. Additionally, ciliary currents and mucus move-

ment may be disturbed by the mere presence of several pereopods and a relatively bulky body on the ctenidial surface. Observed damage to the labial palps, in view of their importance as feeding organs, must certainly have a pronounced effect on the mussel's food gathering ability. Also, in the course of this investigation, several mussels were observed with deep gouges in the mantle and gonadal tissues. These gouges, usually about 1 cm in diameter, were found ventral to the crabs, and it is supposed that they were the result of the latter's presence. PEARCE (1966) attributes similar damage in *Modiolus modiolus* (Linnaeus, 1758) to irritation by *Fabia subquadrata*. While this damage may merely have been the "unintended" result of the crab's feeding activities under normal conditions, as described by ORTON (1921) and MACGINNIE & MACGINNIE (1949), it is not inconceivable that at times of severe food shortage, for example during long, very low spring tides, the crab supplements its diet by including portions of mussel tissue.

That lower zone mussels seem to be unaffected, at least in terms of component indices and glycogen content, by crab-inflicted damage does not serve to nullify the hypothesis that this damage is of consequence to upper zone mussels. High efficiency in food gathering is more likely to be critical when the time for gathering is short, as in the upper intertidal zone, than when feeding times are extended, as they are in the lower zones. Thus, while the feeding efficiency of both upper and lower zone mussels most probably is lessened by damaged tissue, significant effects are observed only in upper zone mussels.

Whatever the specific contributing factors, it is apparent that pea crab infestation of upper tidal zone *Mytilus californianus* produces some predictable deleterious effects:

- 1) The gametic productivity of the testes (and very likely that of the ovaries) is much reduced.
- 2) The viscera index is significantly reduced.
- 3) The entire soft body weight is much reduced from that value expected in an uninfested mussel.

It might be argued that rather than inducing soft body loss in its host, *Fabia subquadrata* instead selectively invades those mussels of proportionally less soft body or differentially survives in the same. This seems unlikely in view of the lack of any such correlation at lower tidal levels.

Glycogen Levels: It was found that the glycogen level of the whole body was lower by 76% in infested mussels of the upper zone when they were compared with their non-infested neighbors. This is consistent with the facts presented above. It is known that in both *Mytilus edulis*

(BAYNE & THOMPSON, 1970) and *M. californianus* a characteristic biochemical response to fasting is a conspicuous reduction of glycogen stores. Also, as mentioned above, anaerobiosis draws heavily on carbohydrate reserves. The pea crab's ingestion of large quantities of polysaccharide-rich mucus likely influences the glycogen level as well. In short, it seems that infested mussels are simply unable to store a normal quantity of glycogen due to the demands of their symbionts.

The evidence presented above in conjunction with that obtained by others indicates a severe nutrient stress is apparently occurring among upper zone host mussels. Low total body weight, gonadal weight, and glycogen levels are indicative of such a situation. Yet it seems highly unlikely that this symbiotic relationship causes a quick death in most mussels, for if death were caused by infestation and consequent starvation, one would expect not to find large, and therefore old, mussels containing large pea crabs because as PEARCE (1966) points out, only young mussels are invaded successfully by *Fabia subquadrata*. Yet relatively large mussels are often found with symbiotic crabs. The evidence seems consistent with the idea that there is some sort of dynamic energetic and nutritional equilibrium between mussel and crab which serves to support both, but the former only in a sub-optimal condition.

If one chooses to use a benefit-harm criterion in deciding the classification of a symbiosis, then the relationship between *Mytilus californianus* and *Fabia subquadrata* must be classified as a case of true parasitism. Not only is the ability of an infested mussel to withstand prolonged energetic stress reduced by a low glycogen level, but also reproductive potential is diminished by decreased gonadal development which persists through spawning.

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